

## DO AMERICAN ROBINS ACQUIRE SONGS BY BOTH IMITATING AND INVENTING?

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**ABSTRACT.**—Although the majority of oscine species acquire a song repertoire by imitating songs they have been exposed to, some species also improvise and invent songs. To test the hypothesis that American Robins (*Turdus migratorius*) both imitate and invent the elements of their whistle songs, I analyzed the song repertoires of wild robins at three locations in western Massachusetts and the song development of five tutor-trained nestling robins. Robins appear to invent or improvise most of the elements in their repertoires (75–82%), but as fledglings and juveniles they acquire the remaining elements by imitating the songs of neighboring birds. Received 29 April 2005, accepted 1 February 2006.

Although it is generally agreed that bird-song serves two basic functions, mate attraction and territory maintenance (Catchpole and Slater 1995), there are striking differences in how various songbirds acquire the songs needed for these functions. In many species, young males imitate only conspecific songs heard during a sensitive period of song acquisition (Marler 1981, Catchpole and Slater 1995). In contrast, several species mimic heterospecific songs (e.g., Northern Mockingbird, *Mimus polyglottos*; Howard 1974, Owen-Ashley et al. 2002). Others not only mimic, but also create new versions of song through progressive modification of previously memorized song, known as improvisation, and/or through invention of entirely new songs unlike anything heard by the young bird (Marler and Peters 1982) (e.g., Gray Catbird, *Dumetella carolinensis*, Kroodsma et al. 1997). There are also species that rely almost entirely on improvisation or invention to develop songs (e.g., Sedge Wren, *Cistothorus platensis*, Kroodsma et al. 1999a). While imitation and mimicry are widespread among all taxa with vocal learning (e.g., dolphins, Tyack 1986; hummingbirds, Baptista and Schuchmann 1990; songbirds, Nelson et al. 1995; parrots, Hile et al. 2000), improvisation or invention has been documented in only a few songbird species (e.g., Nightingale, *Luscinia megarhynchos*, Hultsch and Kopp 1989; Indigo Bunting, *Passerina cyanea*, Payne 1996; Sedge Wren, Kroodsma et al. 1999a, Hughes

et al. 2002) and possibly the signature whistles of dolphins (Sayigh 1990).

It is not understood why some species improvise or invent (Kroodsma 1996), nor is it known how extensive these tendencies are among songbirds or how many times they have evolved. A better understanding of the selective forces for improvising and inventing will emerge only after additional species are studied and only after life history traits are correlated to particular styles of song development. A challenge to such studies is that distinguishing between songs generated by improvisation, invention, or inaccurate imitation is difficult and often rather subjective. To distinguish improvisation from invention, the researcher must be able to document song elements changing over time, from something closely resembling tutor song to songs that may not resemble the tutor song at all. If, however, this period of improvisation is occurring during the winter months when a bird may be only mentally rehearsing song, it would be impossible to distinguish between these two types of song learning.

It has been suspected that American Robins (*Turdus migratorius*) improvise or invent when acquiring song. An early study of robin song found no shared song elements between any of the wild robins studied, even among neighbors (Konishi 1965). Konishi proposed two possible reasons for this lack of shared elements: (1) young robins improvise or invent the elements of their repertoires during the song acquisition phase, or (2) robins learn through imitation, but then disperse to breeding grounds where their song elements are unique (Konishi 1965). Later studies revealed

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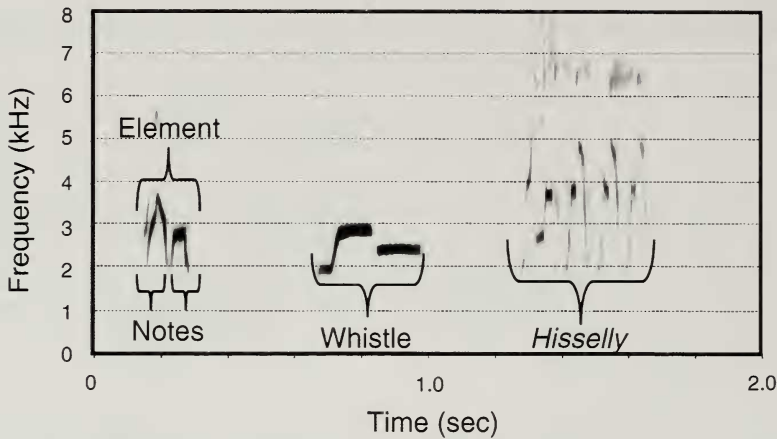


FIG. 1. A representative segment of American Robin song, recorded in western Massachusetts, 2002, showing the various structural units and their associated terms. Notes range from 25 to 250 msec in length and have a frequency range of 300 to 1,500 Hz. Elements range from 150 to 350 msec in length, and can have a frequency range of 1,000 to 7,000 Hz or wider. The time intervals between elements (250 to 2,000 msec) are always longer than the intervals between notes within an element (10 to 125 msec). Whistle elements have a narrow frequency range (mean frequency range =  $1.78 \pm 0.03$  kHz,  $n = 46$ ; Dziadosz 1977), with individual notes ranging from a low frequency of 1.5 kHz to a high of 4 kHz (Dziadosz 1977, Tsipoura 1985; SLJ pers. obs.). *Hisselly* elements have a wider frequency range (mean frequency range =  $4.74 \pm 0.24$ ,  $n = 46$  kHz, Dziadosz 1977) and more rapid frequency modulation (Konishi 1965). Some *hisselly* elements also show evidence of both syrinxes being used simultaneously, as found in other thrush species.

that robins shared one to five elements with neighboring robins (Dziadosz 1977, Thomas 1979, Tsipoura 1985, Sousa 1999), whereas most elements were unique (Tsipoura 1985). The fact that robins share a few elements with close neighbors but not with males from more distant locations (Dziadosz 1977, Sousa 1999) suggests that the shared elements are imitated, but that the unique elements are either improvised, invented, or learned elsewhere. Because of the difficulties in distinguishing between improvisation and invention, I refer to the song learning processes of robins in terms of imitation and invention, but with the understanding that robins may actually be improvising some song elements. Here I provide evidence that robins both imitate and invent/improvise song elements, based on research with both wild populations of robins and hand-reared nestlings.

## METHODS

*Description of robin song.*—The song of the American Robin is composed of sequences of “song elements” that are made up of one or more “notes” shown as continuous markings on a spectrogram (Fig. 1). Male rob-

ins sing two song element types (Konishi 1965, Dziadosz 1977, Hsu 1991). The more common is the familiar whistle-like song usually described as some variation of *cheerily*, *cheer up*, *cheer up*, *cheerily*, *cheer up* (Sallabanks and James 1999). These elements generally sound like clear whistles, but can blend into buzzes or trills. Male robins typically have between 6 and 25 whistle elements in their repertoires (Sallabanks and James 1999; SLJ unpubl. data). The second type of element, described as the *hisselly*, or whisper, song (W. M. Tyler, as quoted in Bent 1949, and Young 1955, respectively), is generally sung very softly and has a much more complex structure. Robins tend to combine both whistle and *hisselly* elements to form groups typically consisting of 3–8 elements (Fig. 2). Although robins have a larger repertoire of *hisselly* than whistle elements, they typically sing whistle elements 5 to 10 times more frequently than *hisselly* elements (Konishi 1965; SLJ unpubl. data). Therefore, I chose to look for evidence of imitation and invention in the whistle elements of both wild and hand-reared robins.

*Recording and analyzing songs of wild rob-*

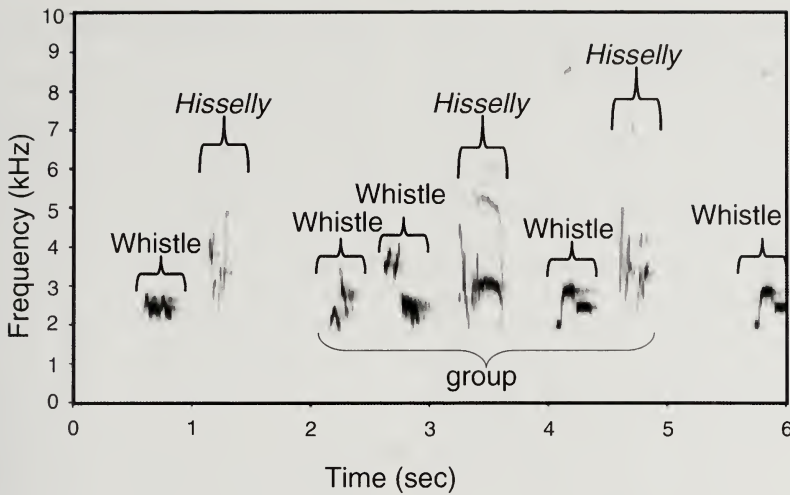


FIG. 2. Spectrogram showing the typical grouping of song elements by an American Robin in western Massachusetts. Robins combine both whistle and *hisselly* elements to form groups typically consisting of 3–8 elements.

*ins.*—I recorded the pre-dawn song of 42 male robins throughout the 2002 breeding season at three locations in Hampshire County, western Massachusetts: 16 birds at the Quabbin Cemetery ( $42^{\circ} 16' 48''$  N,  $72^{\circ} 18' 32''$  W), 16 birds at Mt. Pollux Conservation Area ( $42^{\circ} 19' 39''$  N,  $72^{\circ} 30' 06''$  W), and 11 birds at Wildwood Cemetery ( $42^{\circ} 23' 23''$  N,  $72^{\circ} 30' 44''$  W). The three sites were between 6 and 21 km apart and consisted of open, mowed grassy areas with trees, shrubs, and wooded edges. From 18 April through 4 August 2002, I recorded twice per week at each of the three sites, beginning each day with the first robin song heard, generally 1–2 hr before sunrise, and ending at the first lull in singing after sunrise. Recording typically began at approximately 04:30 EST and ended before 07:00. Recordings were made with a Marantz PMD430 stereo cassette recorder and two Sennheiser ME62 microphones mounted on a Dan Gibson or a Telinga parabola. I attempted to record all the robins singing at each site each day and recorded two birds at a time whenever possible. I attempted to focus on any birds for which I had fewer recordings (i.e., less vocal individuals), and generally limited my recordings of the more vocal birds to 20 to 30 min each day.

I cataloged the song repertoires of individual birds by using field recordings made between 18 April and 16 May. During this pe-

riod, I recorded 1 to 29 bouts per bird (mean = 8.5), with total recording time per bird ranging from 3 to 218 min (mean = 46 min). Because the robins were not banded and I conducted most recording when it was dark, I relied on the precise recording locations and the recordings themselves to determine individual repertoires. I began by noting the location of each bird as I recorded it, and then I determined the repertoire of song elements for each individual recording. I digitized the recordings (sample rate = 23,952.1 Hz) and then printed continuous spectrograms through Signal sound analysis software (Beeman 2003) with the settings as follows: transform length = 256 points, frequency resolution = 93.6 Hz, time resolution = 10.7 msec, and number of transformations = 2000. From the spectrogram of each recording, I determined the song element repertoire. The repertoires were very distinct, each being a unique combination of song elements primarily composed of elements found in no other repertoire. Another distinct feature of each repertoire was the order in which the elements were sung. During each recording of a specific repertoire, certain element combinations were sung much more than would be expected by chance; these combinations were very distinct and consistent over time. I also found that each repertoire of song elements was sung only in a small portion of the recording site. I recorded



each repertoire repeatedly within a specific area, and these areas corresponded to approximate territories of robins observed after sunrise.

To verify that I had sufficient samples of each individual to allow me to determine complete repertoires, I randomly selected 200 sec of recording from each bird for which I had ample recordings, (and 180 sec from the one bird for which I had only 3 min of recording), and next plotted the number of different elements sung over time. In each case, element diversity reached an asymptote after 50 to 100 sec, suggesting that the complete repertoire was revealed. My results were similar to those of Konishi (1965), who found that American Robin repertoires were usually exhausted every 100 elements. During the robin's pre-dawn chorus, an individual will typically sing 100 elements in under 100 sec. The number of song elements revealed within each of the 200-sec samples was the same as the number of elements found for that individual throughout the total recordings made during the first half of the breeding season, and, in most cases, throughout the entire breeding season. Therefore, I feel confident that I had determined the complete repertoire of each bird sampled.

Next, I printed representative spectrograms (11 × 14 cm) of all song elements in each bird's repertoire from the best-quality recordings. Only a few of the elements showed any variability, and these were represented by multiple spectrograms. To assess repertoire overlap among males, five naïve observers were provided with a total of 315 spectrograms representing the song elements from all the recorded repertoires. Observers laid out all spectrograms and sorted the images by general similarities before searching for matching pairs of song elements, which generally took 8 to 10 hr. Identified pairs were then scored—rating their similarity on a six-level scale (0 to 5)—according to written instructions specifying the criteria for each level. A simplified version of the criteria follows: 0 = no similarity; 1 = elements have same general character, but <20% overlap; 2 = elements have some similarity, 20–49% overlap; 3 = elements are similar, 50–79% overlap; 4 = elements are very similar, 80–90% overlap; 5 =

elements essentially the same, 91–100% overlap.

Because of the large number of potential comparisons, it was rare for all observers to identify a specific match; instead, typically two to four observers noted a given match. To ensure that the identified matches did represent very similar song elements, I and one of the original observers scored each match identified by one or more naïve observers, and rejected any matches that did not receive a score of 3 or higher from both of us.

To determine whether robins change their song elements or repertoires within the breeding season, I also evaluated repertoires in a second set of recordings made from 18 June through 4 August 2002. I compared the elements in the repertoires for each individual recorded during these later periods to the repertoires from the beginning of the 2002 breeding season.

*Analyzing repertoire development in hand-reared robins.*—In July 2002, I collected 14 nestling robins (4 to 14 days old) from six nests in Hampshire, Franklin, and Berkshire counties, Massachusetts. The nestlings were hand-reared in an animal care facility at the University of Massachusetts, Amherst, where they were fed a diet adapted from Lanyon (1979). Nest mates were initially raised together in the same cages. Soon after the young robins fledged, I placed each bird in its own cage and divided the birds into two groups of seven, separating siblings as much as possible and attempting to create similar sex ratios in the two groups. The apparent sex of each bird was based on the intensity of plumage color on the head and breast. Male robins generally have darker plumage in both of these regions. There were four apparent males in Group 1, and three males in Group 2. Because female American Robins also sing occasionally (Wauer 1999), I monitored all birds. Each group was housed in a separate isolation chamber (Acoustic Systems, Austin, Texas), and experienced daily periods of illumination mimicking the natural photoperiod.

Each group of robins was exposed to four tutor tapes, each containing the songs of a different wild robin. I created each tape from approximately 10 min of high-quality recording from one of four robins recorded in Amherst, Massachusetts. Each recording was repeated



four to five times to fill one 45-min side of a cassette tape. The tapes were broadcast over two periods. The first tutor period began in August 2002, soon after the youngest birds fledged, at which time they ranged in age from 14 to 40 days; each group was exposed to two of the four tutor tapes during this period. On alternating days, tapes 1 and 2 were played in Chamber 1, and tapes 3 and 4 were played in Chamber 2. Tapes were played for the first 30 min of each daylight period and for 15 min at the end of the day. Each robin heard tutor song for 75 days during this first period.

The second tutor period began in early February 2003, at which time I switched the tapes between the two chambers, exposing the young birds to new song elements. The goal of exchanging the tapes was to evaluate whether the robins imitated sounds heard in their first spring as sub-adults. The young birds began singing on day 21 of this tutor period. I continued to play the tutor tapes for 5 more days and then began recording the young birds.

Using a preamplifier and two microphones, I recorded the young birds with a Nakamichi DR-3 cassette deck. To reduce the chances of recording birds other than the focal subject, I placed 5-cm acoustic foam around each microphone and cage, and, when recording quieter birds, I removed louder birds from the chamber. The young birds were recorded for two 30-min periods each day: the first 30 min of daylight and 30 min after feeding, when the birds often increased their rate of vocalization. I recorded the birds for 62 days from late February to early May.

Five of the birds identified as males produced song elements similar to those of wild robins; the remaining birds made only call notes. Four of the singing birds were in Group 1, and one was in Group 2. Two of the singing males in Group 1 were nest mates, while a third bird had a nest mate in Group 2. The song elements in each bird's repertoire remained stable throughout the 2.5-month recording period, and so appeared to represent crystallized song.

I digitized the recordings of the hand-reared birds and the tutor tapes, sampling at a rate of 20,000 Hz. I selected a representative example of each song element from each robin, and printed spectrograms using the same methods

described above for the field recordings. Five naïve observers compared 331 representative spectrograms from the hand-reared and tutor repertoires. The same conditions and criteria for scoring similarity were followed as described above.

To determine whether the young robins had imitated adult song heard near their nest sites prior to capture, I compared each young bird's repertoire to that of adult robins ( $n = 3$  to 6) from each nest site, as assessed from recordings made on the morning of capture or the day after. Representative spectrograms were printed and scored for similarity by two naïve observers, as described above. Means are presented  $\pm$  SD.

## RESULTS

*Element similarity, repertoire delivery, and stability in wild robins.*—Males from the same sites shared more song elements than those from different sites (Mann-Whitney test:  $P < 0.001$ ,  $n = 42$ ), suggesting that robins imitate some of the elements of local robins. The naïve observers identified 59 element pairs out of a possible 49,455 pairs, for which a majority of observers gave a similarity score of 3 or higher. Fifty-six of these identified pairs represented birds from the same recording site; their average similarity score was 3.7. The remaining three pairs represented elements recorded at different locations; no observer, however, gave a score higher than 3 for these pairs, and their average similarity score was 2.3. All matches found between multiple representatives of a single element type from within-bird repertoires were scored 4 or higher by the observers. Thirty-six of the 42 birds shared elements with other birds within their site. The percentage of elements in a bird's repertoire that were similar to elements in other repertoires at the same site ranged from 0 to 50% (mean =  $25 \pm 15\%$  SD). In contrast, only five birds had elements that were judged as similar to elements of birds from different locations (Fig. 3). In each bird's repertoire, the percentage of elements that were similar to elements in the repertoires of birds from different sites ranged from 0 to 16.6%.

Most elements within each bird's repertoire were judged to be unique to that individual (mean =  $75 \pm 15\%$  SD), indicating that the

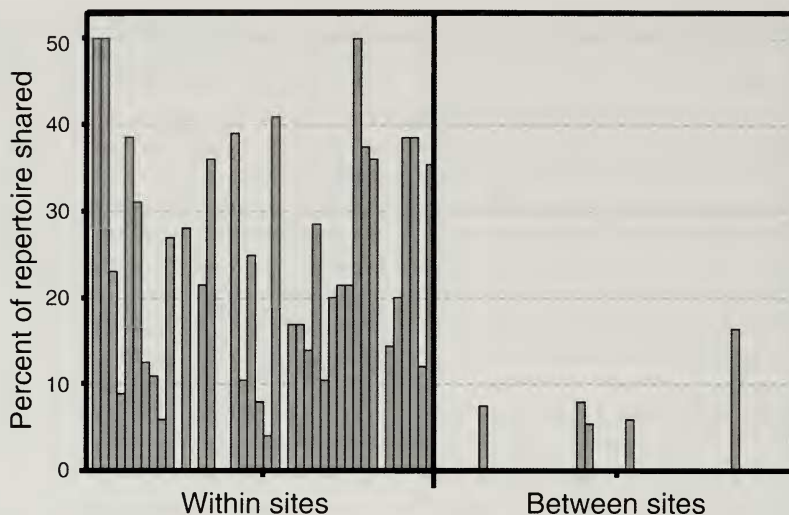


FIG. 3. Comparison of the percent of each American Robin repertoire shared within and between three sites in western Massachusetts, 2002. Each bar represents a single robin's repertoire. American Robins share far more elements with neighboring robins than with robins from different sites. The percent of shared elements in the repertoires of 42 robins is shown for both within and between sites. Note that 37 of 42 birds share 0% of their repertoire with birds from other sites.

robins either invented most of their song elements, learned them elsewhere, or learned them from a bird no longer present. In later recordings, these unique elements made it possible to identify each bird by its songs alone. The repertoires recorded during both the early and late periods retained the majority (mean =  $98 \pm 14\%$ ;  $n = 15$  birds) of their elements throughout the entire season. However, the repertoires of six well-sampled birds ( $>440$  sec of recording each period) did appear to change. One to two elements were added to two repertoires, and one to four elements were dropped from four repertoires. Two of these fluctuations may have been artifacts of unequal recording time between the two periods (i.e., the increase or decrease in repertoire size paralleled the increase or decrease in sample size between the two time periods), but the remaining four repertoire changes trend in the opposite direction from changes in the sample sizes between the two periods. For example, four of the elements in bird W3's early repertoire were missing in the later repertoire, despite an increase in recording time. Conversely, a new element was found in the late repertoire of Q3, despite a 97% reduction in recording time.

Some robins clearly modified individual el-

ements over the course of the breeding season. Birds P6 and Q5 each sang one element that changed over the course of the breeding season (Fig. 4). In both cases, the new form completely replaced the old form. What was particularly striking about the change in Q5's case was that the later version was a much closer match to elements in three other repertoires from the same location (Fig. 5).

*Song learning in hand-reared robins.*—The tape-tutoring experiment provided evidence of both invention and imitation during song learning. The percentage of shared elements varied greatly among the five hand-reared robins that produced song. Two nest mates shared between 55.5 and 65% of their repertoires with each other, two other birds in this group, and the tutor tapes, whereas there were fewer shared elements in repertoires of the remaining three birds (range = 0–30%, mean =  $14 \pm 15\%$  SD). There was almost no evidence of imitation of songs heard at the nest; one element of a single hand-reared bird was considered similar (average score 3) to an element recorded at that bird's nest site. These may have matched by chance, since both elements were simple descending whistles.

The remaining elements produced by the five birds did not match elements from the

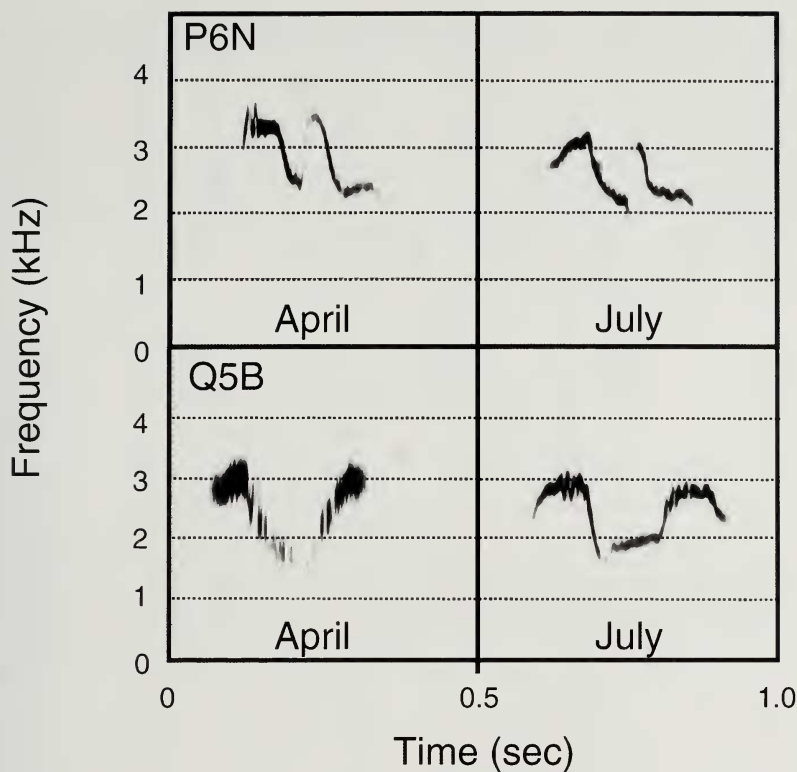


FIG. 4. Modifications of song elements over time from two wild American Robins (P6, element N; Q5, element B). Subjects were recorded in April and July 2002 in western Massachusetts.

nest sites, the tutor tapes, or other hand-reared birds, suggesting that the unique elements were either improvised or invented (Marler and Peters 1982, Nowicki et al. 2002). I compared examples of these elements at different times throughout the 62-day recording period and found no change over time, suggesting that the unique elements were invented, rather than improvised; however, I cannot eliminate

the possibility that the young birds improvised changes during the winter silent period or before I began recording. I also compared the elements produced by the hand-reared birds to spectrograms of Konishi's (1965) isolated and deafened robins. I found that the elements produced by my hand-reared birds showed little or no within-element variability and consisted of whistle notes similar to those of wild

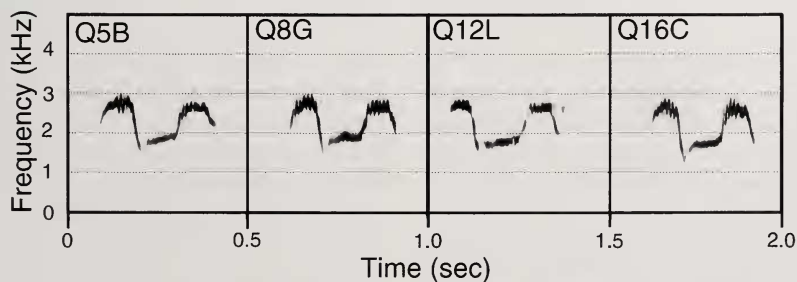


FIG. 5. Song elements of four American Robins recorded at the Quabbin Cemetery in Hampshire County, western Massachusetts, 2002. The late (July) version of bird Q5's element B is a closer match to elements in three local birds' repertoires than the early (April) version of bird Q5's element B in Figure 4.



TABLE 1. The number of song elements that four hand-reared birds (A2, F1, D1, and D2 in columns) within one isolation chamber shared among themselves and two tutor tapes (T1A and T1B). The highest incidence of sharing was between hand-reared siblings D1 and D2. F1 did not share any elements with two siblings raised in a separate chamber. All birds were reared and/or recorded in western Massachusetts, 2002.

Bird ID	A2	F1	D1	D2
T1A	1	1	0	0
T1B	0	1	0	0
A2	—	0	1	0
F1	0	—	3	2
D1	1	3	—	15
D2	0	2	15	—

robins, whereas Konishi’s birds produced songs with a high degree of within-element variability; elements consisted of wavering whistle notes. This suggests that the song elements produced by the hand-reared birds were fully crystallized, invented/improvised songs, rather than the basic acoustic features of song that can be produced by isolated birds.

Although most of the elements were invented/improvised, imitation was also evident in four of the young birds’ repertoires. The young birds tended to share more elements with other hand-reared birds than with the tutor tapes (Table 1). The naïve observers identified 24 pairs of elements, the average similarity scores of which were  $\geq 3$ , indicating a high degree of similarity. Fifteen of the 24 identified pairs were between two siblings housed in the same chamber (see Fig. 6 for examples). Two of the elements shared by these siblings were also sung by non-siblings housed within the same chamber. Six pairs were between non-siblings within the same chamber, and three pairs were between tutors and young birds (see Fig. 7 for example). The imitated tutor elements were from tapes played only during the first tutoring period, whereas the elements shared between birds could not have been heard until the birds were old enough to sing. No elements were shared between the birds in Group 1 and the single singing bird in Group 2, even though this bird had two male siblings in Group 1.

The percentage of shared elements in each bird’s repertoire varied greatly. Bird A2

shared 30% of its repertoire, Bird D1 65%, Bird D2 55.5%, Bird F1 13%, and Bird F2 0% (mean =  $32.8 \pm 27.5\%$  SD). The degree of sharing in A2, F1, and F2 falls within the range of sharing I found for wild robins; however, that of the siblings D1 and D2 was much greater due to the percentage of elements they shared with each other (63% and 42%, respectively).

DISCUSSION

The field recording and tape-tutoring components of this study indicate that American Robins can and do imitate song elements. Among repertoires of wild robins, closely matching song elements were found within sites, but only weak similarities were found between sites, indicating that the matching elements were imitated. Additional evidence of imitation was found in the case of one bird at the Quabbin site that changed one element to more closely match an element shared by three other birds from that site, indicating that robins can change their repertoires to match other birds. Because the ages of the recorded robins were not known, it has yet to be determined whether this ability is restricted to the first breeding season.

A similar pattern was found in the repertoires of hand-reared birds, which together produced three close matches to elements from tutor tapes. In addition, birds kept within a single chamber produced 21 closely matching elements, but there were no matching elements between birds raised in separate chambers. The fact that the 21 matching elements between birds could not have been learned until the birds began singing also supports the idea that adult robins—at least in their first breeding season—can change, or add to, their repertoires. Closely related Blackbirds (*Turdus merula*) also appear to continue learning songs as adults (Rasmussen and Dabelsteen 2002). A possible limitation on the interpretation of these results is that tutor tapes, rather than live tutors, were used, and the stimulus of live tutors, as experienced in nature, may elicit a higher degree of imitation.

Robins may have a tendency to learn song elements that are heard more often, either because they are sung by multiple birds, or are sung by a highly vocal bird. My data offer some support for this tendency. Two of the

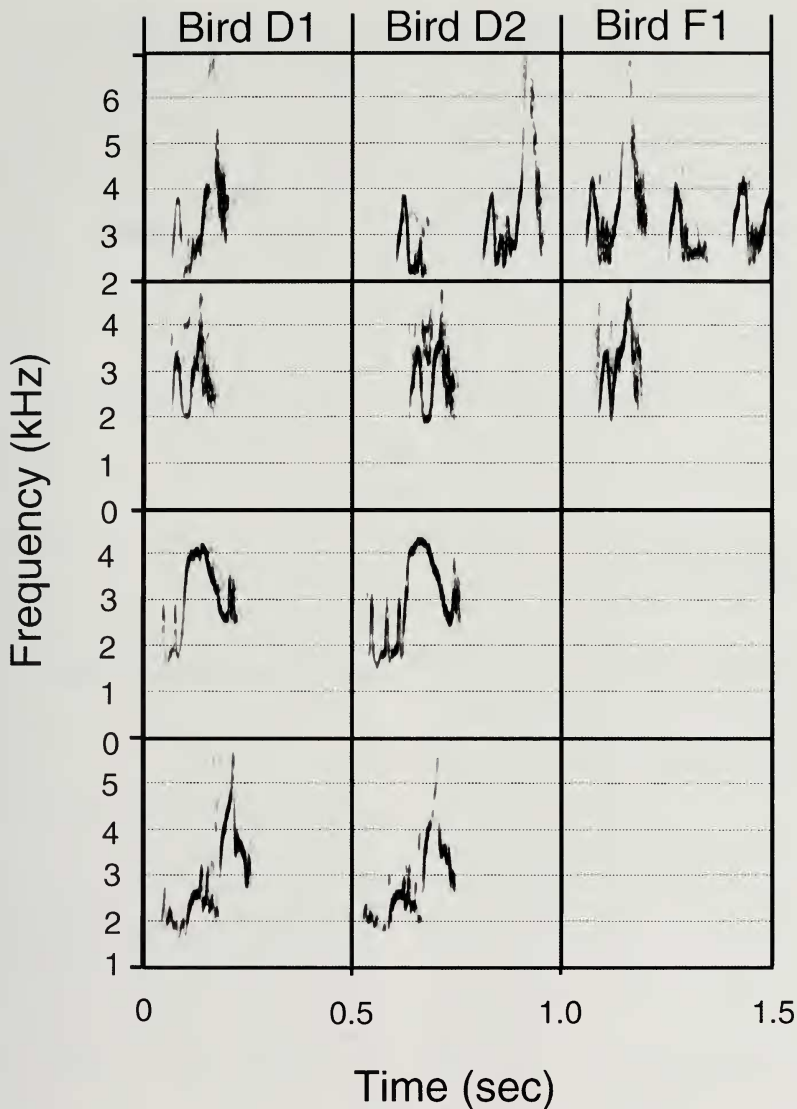


FIG. 6. Four examples of song element sharing between three hand-reared American Robins raised in one chamber in western Massachusetts, 2002. Birds D1 and D2 are brothers and shared more elements than any other hand-reared birds. The lower two elements were shared only by D1 and D2, not by F1.

song elements sung by the hand-reared robins were shared by three individuals, and many of the elements shared by wild robins were shared by three or more individuals. It also appears that one wild robin altered one element in his repertoire to more closely match that of three other robins within his particular recording area.

Robins also appear to invent or improvise song elements. The majority of elements produced by the tape-tutored birds were unique

for each individual, indicating that the elements were invented/improvised by the tutored birds. The majority of elements in the wild robin repertoires were also unique to each individual, which suggests that invention or improvisation also could be involved in song acquisition in the wild. However, I cannot rule out the possibility that at least some of these elements may have been learned elsewhere or from birds no longer present at the local site.

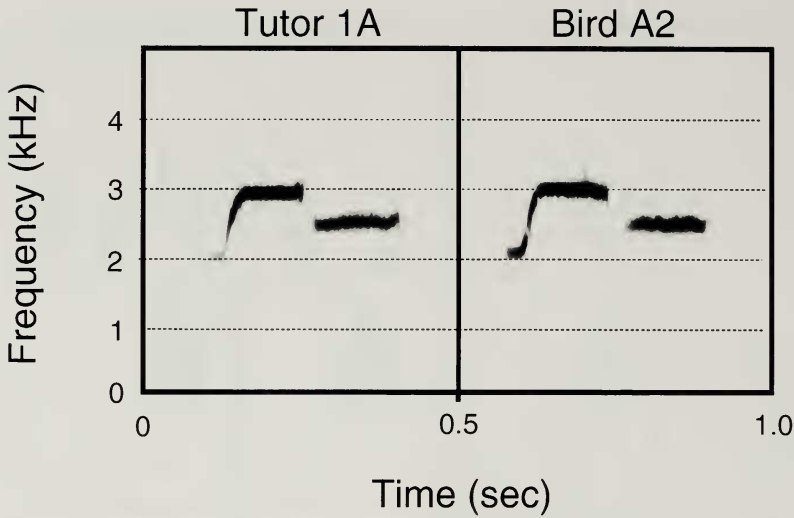


FIG. 7. Example of song element matching between tutor tape 1A and hand-reared American Robin A2, western Massachusetts, 2002.

My results are not completely consistent with either of Konishi's (1965) hypotheses on robin song development. Konishi found no evidence of element matching, and he explained this by suggesting that either robins improvise/invent the elements of their repertoires during song acquisition, or they learn through imitation and then disperse to breeding grounds where their song elements are unique (Konishi 1965). My results suggest that robins do improvise/invent songs, but also imitate songs of nearby robins, and that these imitations occur during both early song acquisition and after robins settle on breeding territories, allowing adult birds to share song elements with local males.

Song sharing plays an important role in the communication of several species. For example, neighboring males in many species song-match during territory defense as a warning of potential escalation (Krebs et al. 1981, Falls et al. 1982, Beecher et al. 2000a). A benefit of this system is illustrated in Song Sparrows by the positive correlation between how long a male holds a territory and his ability to share songs with his neighbors (Beecher et al. 2000b). Robins also may benefit from sharing elements in their repertoire; although they may not song-match, most robins sing the shared elements in their repertoire more than would be expected by chance (SLJ unpubl. data). It is also worth noting that only three

robins recorded during the first third of the breeding season did not share elements with other birds at their sites, and that none of these birds could be found in the last third of the season.

The results of my tape-tutoring experiment indicated that social interaction with live birds provided stronger stimulation for imitation than tutor tapes—as found in many studies (e.g., Beecher 1996), suggesting that the benefit of sharing elements is tied to social interactions. A particularly interesting result of this experiment is the high percentage of element sharing between the two siblings with visual and acoustical access to each other. This contrasts with the lower percentage of sharing with other, equally accessible birds in the same chamber, and with the complete lack of sharing between the siblings raised in different chambers. It appears unlikely that this high degree of sharing is a result of songs learned and imitated from parents or neighbors during the nestling period. One possible interpretation is that there is a predisposition to learn from one's relatives (Nelson and Marler 2005). Further research into the social interactions between adult and fledgling robins, particularly between closely related birds, may provide additional clues to the importance of shared elements in American Robins.

Why American Robins both imitate and invent during song development remains a mys-



tery. A key to unraveling this mystery is the fact that song development evolves in response to selection pressures brought about by other life-history traits (Kroodsma 1983). For example, some highly migratory or nomadic species tend to improvise or invent a higher percentage of their songs than closely related species and subspecies that are non-migratory and/or exhibit greater philopatry (Kroodsma et al. 1999a, b; Nelson et al. 2001; Handley and Nelson 2005). We can address the question of why a species invents and/or imitates by looking for correlations between song development and life-history traits (e.g., migratory status, philopatry) among closely related groups (e.g., Read and Weary 1992, Nelson et al. 1995). The American Robin, with seven subspecies, including one that is non-migratory, promises to be an excellent subject for such a comparative study. With 65 congeners (Phillips 1991), the robin could also be part of a much broader study that incorporates a wide range of traits in song development and life history.

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